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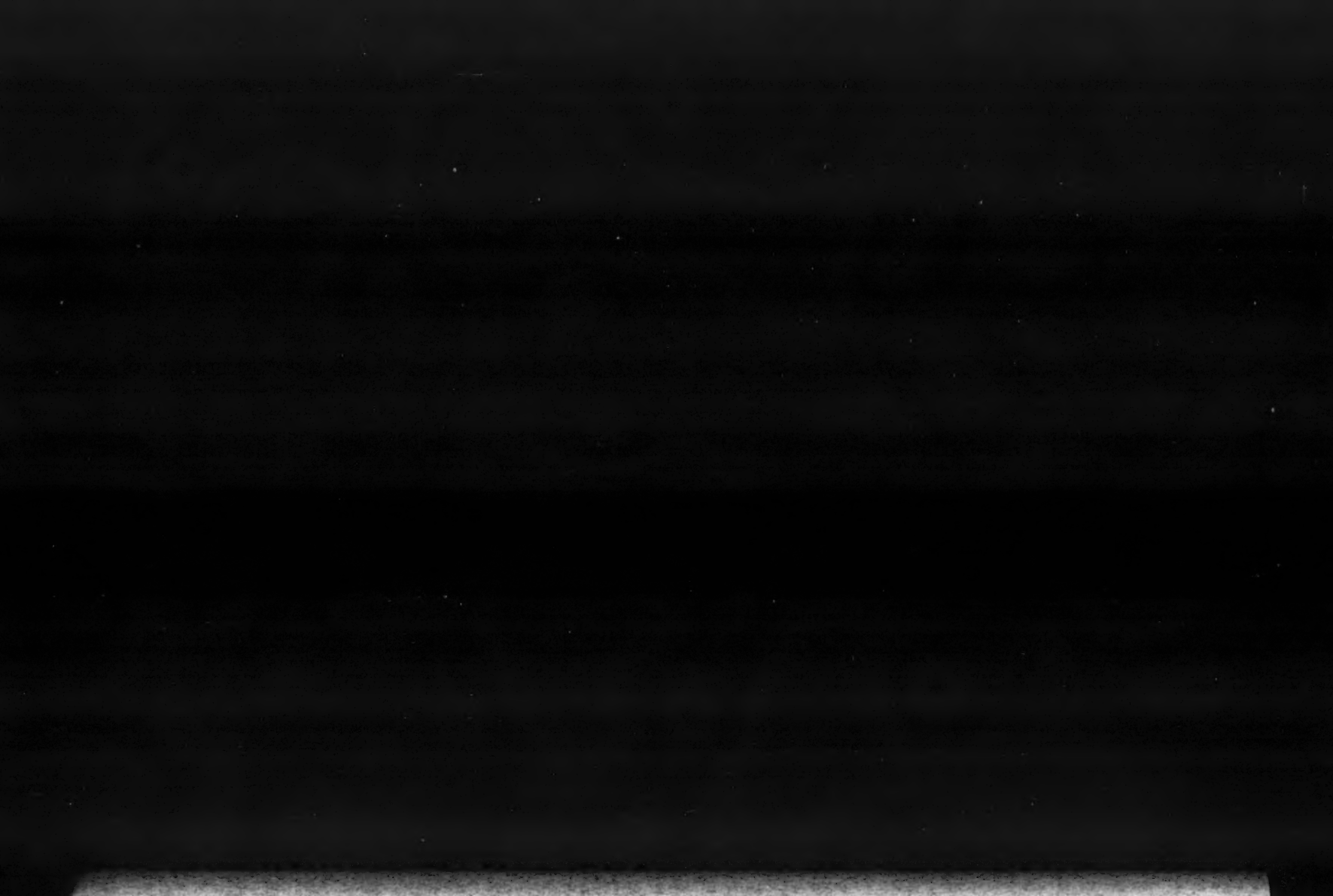

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BIOLOGICAL BULLETIN

STUDIES IN MARINE ECOLOGY: III. SOME PHYSICAL FACTORS RELATED TO THE DISTRIBUTION OF LITTORAL INVERTEBRATES.

W. C. ALLEE,

MARINE BIOLOGICAL LABORATORY AND THE UNIVERSITY OF CHICAGO.

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I. PURPOSE AND SCOPE OF THE INVESTIGATION.[1]

The first two papers in the present series give the results of a general faunistic ecological survey of the Woods Hole littoral

[1] I am indebted to the Marine Biological Laboratory for facilities for carrying on this survey and particularly to Mr. G. M. Gray for arranging for my comings and goings. I am also indebted to Dr. P. H. Mitchell of the Bureau of Fisheries for the loan of certified hydrometers and to Supt. W. H. Thomas for access to manuscript notes of daily temperature and salinity determinations.

region which occupied the summers of 1913–1921 inclusive. The records given there show the distribution of the common littoral invertebrates and discuss the relationships of the different animal associations present on the basis of their animal components.

The present paper deals with the results of an intensive study of some of the localities considered in the preceding sections, which was carried on in August and early September of 1920, with some additional data from records taken the following summer. In addition to considering the direct effects of different types of bottom and shores, currents, tides and vegetation, this study is particularly concerned with the possible correlation of temperature, salinity, oxygen content and pH with the intertidal and upper adtidal animal associations of the region immediately around Woods Hole.

Reference to the map published in connection with Study I. of this series will give the general location of the region and the *Biological Survey*[1] (pp. 170–190) gives a good account of the general physiographie features. The more important of these for the purpose of our discussion are:

1. The whole region lies far back from the edge of the continental shelf. The 20 fathom line runs 10 miles off Martha's Vineyard while the 100 fathom line, marking the edge of the continental shelf, is 75 miles from Gayhead and about 90 miles from Woods Hole.

2. The unequal height of the tides in Buzzards Bay and Vineyard Sound combined with the time difference of tides in the two bodies cause strong currents to flow almost incessantly from one to the other. All the localities discussed in this paper are directly affected by these tidal currents except the wharf pilings at Vineyard Haven and the bay at Gansett.

3. There is a general westerly drift in the region so that the *Biological Survey* estimates that all the water in Vineyard Sound is renewed weekly and in Buzzards Bay in about double that time.

4. The temperature is influenced by the Gulf Stream although his is normally shut from shore by a wall of cold water. The water immediately around Woods Hole is warmer in summer

[1] Sumner, Osburn and Cole: A Biological Survey of the Waters of Woods Hole and Vicinity. Bul. Bur. Fish., Vol. 31.

and probably cooler in winter than outlying waters.[1] The *Biological Survey* reports an annual temperature range of 25° C. at the Fish Commission pier where the water is much mixed by the current through the Hole. The range is greater in stagnant water such as that in Blind Gutter at Lackey's Bay where the annual range is over 33° C.[2]

5. The intertidal zone is comparatively narrow, being more extensive in Buzzards Bay than in Vineyard Sound.

6. The shores of the region are usually lined with rocks which extend well below the low tide level and give way there to sandy bottoms in the more exposed places. In sheltered regions mud of organic origin is deposited over the sand.

7. The *Biological Survey* found that the salinity of Buzzards Bay averaged 3.00 per cent.; that of Vineyard Sound, 3.075 per cent. The open Atlantic runs to 3.6 per cent. or more.[3]

During the investigation the open water was sampled in four inshore localities:[4] Off the Buzzards Bay entrance to N. W. Gutter (Map, No. 10), in the Hole at Woods Hole; in Vineyard Sound at the entrance to Lackey's Bay (Map, No. 6) and at the entrance to Gansett Bay (Map, No. 11).

The wharf pilings were studied at Crane's Wharf (Map, No. 5) near the steamboat wharf in Woods Hole and at the old steamboat wharf in Vineyard Haven (Map, No. 1). The rocks at Northwest Gutter near its Bay entrance (Map, No. 10), in Lackey's Bay at the entrance to Blind Gutter Flats (Map, No. 6) and at Gansett. The associations of the flats were studied at Northwest and Blind Gutters and at Gansett, together with some observations in the creek leading to Southwest Gutter. In all 122 sets of collections were made.

These localities were chosen for intensive study because they are typical of the region and because of their proximity to and ease of access from the laboratory.

[1] Cf. discussion in Biological Survey, pp. 37 and 50.

[2] Water over the eel grass in Lackey's Bay had a temperature of 32 deg. C. on the afternoon of August 15, 1920. There is no reason to suppose that this temperature is unusual. In winter the temperature must frequently fall below the freezing point of sea water.

[3] See Murray and Hjort.

[4] For descriptions of the different habitats see Study I. of this series.

II. Methods.

The water collections for oxygen samples were usually made according to the method given in Standard Methods for Water Analysis.[1] Where this method was impracticable, as in surface collections, the sample was taken by means of a two-valve rubber bulb. In all cases more than four times the amount of water necessary to fill the sample bottle was run through it before the sample was taken.

The oxygen determinations were by the Winkler method. The chemicals were added and the titrations were made in the field.

Salinity was ascertained by the specific gravity method with standardized bulbs loaned by Dr. Mitchell of the U. S. F. C. The salinity is expressed in the tables as calculated from the specific gravity according to the data given by True (1915).

The pH was determined colorimetrically by comparison on the spot with standard colors in tubes specially prepared for salt water by Hynson Westcott and Co. Two indicators were used mainly: Thymolsulphonephthalein (thymol blue) with a color range from 8.0 to 9.6 and dibromthymolsulphonephthalein (bromthymol blue) ranging from 6.0 to 8.0. These sets of standard colors were made up in June before they were used in August.[2] Doubtful determinations in the 7.7–8.0 range were tried with both indicators and on occasion with phenolsulphonephthalein, range 6.6–8.6. This last set of standard colors were made up in distilled water. Such readings were corrected for sea water by subtracting 0.1 from the observed reading.[3] Comparative readings with this correction applied are given in Table I.

The water for pH determinations was collected in a new 40 c.c. injecting syringe with a tight-fitting piston, either directly from the surface or from the large container of the standard apparatus used in collecting oxygen samples. This water was also used in

[1] Report of the Committee on standard methods of water analysis. Jour. Inf. Diseases, Suppl. No. 1, pp. 1–141.

[2] The dibromthymolsulphonephthalein set was loaned me by Dr. E. B. Powers in 1920 and by Miss Myra Sampson in 1921.

[3] Atkins ('22) reports the salt error to be almost double that found here.

finding temperatures from some depth below the surface. All determinations were ordinarily made in duplicate and, oxygen excepted, frequently in triplicate.

TABLE I.

SHOWING COMPARATIVE RESULTS OF USING THREE INDICATORS IN DETERMINING THE pH OF SEA WATER.

Indicator.	I.	II.	III.	IV.	V.
Dibromthymolsulphonephthalein.....	8.0 +	8.0 +	8.0 +	7.3	8.0 +
Thymolsulphonephthalein.....	8.0 +	8.0 +	8.2	8.0 −	8.2
Phenolsulphonephthalein.....	8.0 +	8.0 +	8.2	7.3	8.2

III. SERIES OF ASSOCIATIONS.

The animal associations of the Woods Hole littoral can be divided into two series either on the basis of the character of the bottom, or of physiographic action. On either basis the resulting series are the same, for the eroding shores of the region are all rocky and the depositing shores have a shifting bottom composed of mud or sand. Within these series the associations may readily be arranged in the order of their physiographic age.

The associations of the rocky eroding shores as studied are: (1) open water; (2) wharf pilings; (3) exposed rocks; (4) protected rocks. The associations of the depositing shores likewise begin with (1) the open water and typically continue as follows: (2) those of the sand bar; (3) with the deposition of mud this becomes the muddy sand association in which eel grass begins; (4) with further deposition of mud and as the eel grass grows longer one finds the *Cumingia* association and in deeper water where still more muck has been deposited, the *Scoloplos acutus* association. These make up the two main associations of the eel grass and muck, which extend to the margin of the eel grass in about a foot of water at low tide. Between this level and the shore at about low tide lies the marginal muck association (5) which gradually gives way to the intertidal associations, the lower of which may be called the *Mya* association and occupies the region from just below low tide to about the half tide mark. The upper association is marked by the abundance of the snail *Melampus* and may well be called by that name. In places the *Ucas* are more abundant, but such localities have not been studied in this report.

In order to understand this typical arrangement of associations in the depositing shore series it is necessary to know that in the flats of the region there is usually a sand bar formed at the outer edge of the flat which is frequently uncovered at low tide; farther back on the flats the water becomes slightly deeper in the region of mud and sand and then decidedly deeper until one reaches the *Scoloplos acutus* association of the eel grass and muck region. As one nears the shore the water becomes shallow again.

While the series as given is typical of the region there are several other possibilities which will be discussed in their proper places.

1. *The Rocky Eroding Shore Associations.*

a. The Open Water Association.—The results of analyses of water samples from four inshore stations are shown in Table II.

TABLE II.

SHOWING SALINITY, TEMPERATURE, OXYGEN CONTENT AND pH OF OPEN WATER FROM INSHORE STATIONS.

Date.	Time.	Depth Ft.	Tide.	Temp. ° C.	pH.	O. in c.c. per L.	Salinity ‰.	Light.	Coll. No.
1920					I.				
8/16	10:50	14	High	21	8.0	—	—	Dull	11
	11:10	22	High	21	8.0	3.93	—	Dull	12
9/3	9:15	22	Do.	20	8.0 −	4.37	3.02	Bright	107[1]
							3.05		
					II.				
8/16	4:00	15	Sound to Bay	22	8.0 +	—	—	Dull	22
	4:10	10	Do.	22	8.0	—	—	Dull	23
1921									
9/12	11:45	12	Do.	21	8.0	5.43	3.14	Dull	122
					8.0	5.38	3.14		
				21	8.0	5.38	3.14		
					8.0	5.38	3.14		
				21	8.0	5.35	3.14		
				21	8.0	5.38	3.14		
				21	8.0	5.35	3.13[2]		
					8.0	5.33	3.12[2]		
					8.0	5.38	3.12[2]		
					8.0	5.38	3.12[2]		
					III.				
1920									
9/3	5:00	12	Bay to Sound	21	8.1	—	3.04	Bright	120
					IV.				
8/31	4:10	24	Low	22	8.2	6.14	—	Rainy	100
	4:10	24	Low	22	8.0	5.84	3.09	Rainy	100′

[1] Collection 7 feet down.
[2] Determination in laboratory.
[3] Collection made 12 feet down.

Part I. is from collections made off the Bay opening of Northwest Gutter about 75 yards directly west of the corner of the channel made by the shoulder of Uncatena Island. Part II. is from the passage in Woods Hole and the third part is from the opening of Lackey's Bay into Vineyard Sound. The latter is influenced by the current carrying water from the extensive submerged vegetation of this region. Part IV. is from the mid-mouth of Gansett Bay. The surface water here also shows the effect of proximity to vegetation. The depths are those given in the U. S. Coast and Geodetic Survey charts. The last two divisions are given for comparison only and will not be considered in discussing open water conditions since they are obviously atypical.

The invertebrate animals to be found near the surface in such locations are largely plankton. A typical collection taken with miller's bolting cloth net from a Bay tide in Woods Hole at 10:00 A.M., August 8, 1917, is shown in List 1. The collection was studied the afternoon after it was taken by the class in Invertebrate Zoölogy of the Marine Biological Laboratory with the assistance of seven instructors. The list is based on the findings of approximately sixty people in a two hours search.

LIST 1. SHOWING THE MORE CONSPICUOUS ANIMALS TAKEN IN ONE TOWING IN THE HOLE.

Animals.	Number Found.	Animals.	Number Found.
PROTOZOA		BRYOZOA	
Ceratium	8	*Cyphonautes*	5
CŒLENTERATA		CRUSTACEA	
Actinula of *Tubularia*	2	*Nauplius*	3
Hydromedusæ	12	*Zœa*	5
NEMERTINI		*Mysis*	4
Pilidium of *Cerebratulus*	1	*Megalops*	5
CHÆTOGNATHA		Copepoda	∝
Sagitta	2	*Cypris* larvæ of *Balanus*	1
ECHINODERMA		MOLLUSCA	
Bipinnaria	12	Lamellibranch veligers	4
Brachiolaria	5	Gasteropod veliger	∝
Pluteus	2	CHORDATA	
ANNELIDA		*Appendicularia*	14
Dinophilus	5	*Botryllus* tadpoles	1
Trochophores	2		

b. Wharf Piling Association.—The animals in this association, whether free living, attached, or living among attached forms, are more abundant at the outer end of the piers where the water

is deeper and the wave action is less violent. The conditions in the water, so far as investigated, are given in Table III. It will

TABLE III.

SHOWING SALINITY, TEMPERATURE, OXYGEN CONTENT AND pH OF WATER FROM WHARF PILINGS ASSOCIATION.[1]

Date 1920.	Time.	Depth in Ft.		Temp.	pH.	O_2 in c.c. per L.	Salinity.	Collection Number.
		Water.	Collection.					
8/21	8:30	12 +	12	19	8.0	4.48	—	40
	8:45	12 +	1	19	8.0	—	—	40
	9:20	10	10	20	8.0	—	2.97	41
	9:40	1	1	20	8.0	—	—	42
	10:10	12 +	0.25	—	—	6.0	—	43
8/22	9:40	12 +	1	20	—	4.36	—	44
	9:40	12 +	1	20	—	4.26	—	45
	10:00	12 +	12	20	—	4.16	—	46
	10:00	12 +	12	20	—	4.26	—	47
	10:35	12 +	1	—	—	4.11	—	48
	10:35	12 +	12	—	—	4.06	—	49
8/28	3:30	1	1	21	8.0	5.25	3.01	85
	3:45	12 +	12	20	8.0	5.25 5.15	3.07	86
	4:00	12 +	1	21	8.0	5.25	3.13	87

be noted that the pH was constant in all locations; that the oxygen content was relatively constant for each location, with the exception of one collection taken at Crane's Wharf just after the passing of a Nantucket steamer which caused a decided increase. There is no evidence of vertical gradients among the factors analyzed to explain the vertical distribution of animals found on the wharf pilings; nor is there an indication of horizontal gradients along the wharf save in salinity.

All the animals found in collecting on Crane's Wharf pilings are given in List 2. The figures give an arbitrary means of showing relative abundance and are based on the number of collecting teams reporting each animal in one afternoon's work early in July, 1920. Absence of such figures shows that the animals were not found at that time.

[1] Low tide and bright sunlight throughout.

LIST 2. SHOWING THE INVERTEBRATE ANIMALS TAKEN FROM CRANE'S WHARF PILES IN NINE YEARS' COLLECTING.

The figures give an indication of comparative abundance in 1920 and are based on the number of collecting teams reporting the several species. Absence of figure indicates that the animal was not taken during this trip.

	Sessile	Free
PORIFERA		
Chalina arbuscula	7	
Cliona celata(?)	7	
Grantia ciliata	7	
Leucosolenia botryoides	5	
Microcione prolifera	7	
CŒLENTERATA		
Campanularia sp.	1	
Clytia bicophora	7	
Eudendrium album		
Eudendrium ramosum		
Gemmaria gemmosa	1	
Hydractinia echinata		
Metridium dianthus	6	
Obelia commissuralis	4	
Obelia geniculata		
Pennaria tiarella	1	
Sagartia luciæ	1	
Sagartia leucolena	1	
Schizotricha tenella		
Sertularia pumila		
Tubularia crocea	7	
PLATYHELMINTHES		
Tetrastemma vermiculum	1	
Lineus bicolor		
NEMATHELMINTHES		
Pontonema marinum	5	
ECHINODERMA		
Arbacia punctulata		3
Asterias forbesi		5
Asterias vulgaris		1
Henricia sanguinolenta		
ANNELIDA		
Arabella opalina		1
Amphitrite attenuata		2
Autolytus cornutus		1
Harmothæ imbricata		5
Hydroides hexagonus	5	
Lepidonotus squamatus		7
Lepræa rubra		
Nereis pelagica		7
Nicolea simplex		2
Podarka obscura		2
Polycirrus eximeus		3
Polydora sp.		
Phyllodoce catenula		
Sabellaria vulgaris		
Spirorbis spirorbis	6	
Sthenelais leidyi		
Thelepus sp.		
BRYOZOA		
Ætea anguina	5	
Bugula turrita	7	
Bicellaria ciliata		
Crisia eburnea	7	
Lepralia pertusa		
Membranipora pilosa	6	
Flustrella hispida	2	
Schizoporella unicornis	6	
ARTHROPODA		
Amphithæ rubricata		2
Autonæ smithi		1
Anoplodactylus lentus		2
Balanus balanoides		7
Balanus eburneus		2
Caprella geometrica		7
Erichsonella filiformis		1
Idothea baltica		2
Libinia dubia		6
Libinia emarginata		6
Lygidia oceanica		2
Orchestia agilis		
Palæmonetes vulgaris		
Palene empusa		1
Pinnotheres maculata		2
Panopeus sayi		6
Talorchestia longicornis		
Tanystylum orbiculare		2
MOLLUSCA		
Acmea testudinalis		1
Anomia aculeata	1	
Anomia ephippium	4	
Arca pexata		
Biltium alternatum		4
Busycon carica		
Columbella avara		6
Columbella lunata		7
Crepidula convexa		
Crepidula fornicata		3
Crepidula plana		3
Coryphella gymnota		5
Lacuna vincta		4
Littorina litorea		7
Littorina palleata		1
Littorina rudis		1
Modiolus modiolus	1	
Mytilus edulis	6	
Teredo navalis		3
Odostomia sp.		
Urosalpinx cinereus		7
CHORDATA		
Amaræcium constellatum	6	
Botryllus schlosseri		
Didemnum lutarium	7	
Molgula arenaria	1	
Molgula manhattensis	4	
Molgula papillosa	1	
Perophora viridis	6	
Styela partita	7	

Table IV. shows data taken from the records from the U. S.

TABLE IV.

SHOWING TEMPERATURE AND SALINITY FROM THE NOON READINGS OF THE U. S. FISH COMMISSION AT THEIR WOODS HOLE WHARF FOR AUGUST, 1920.

The raw data in sp. gr. and Fahrenheit have been converted to percentage of salinity and the centigrade scale for purposes of comparison.

Day.	Salinity.	Temperature.	Day.	Salinity.	Temperature.
1	3.20	21.7	16	3.22	22.2
2	3.19	20.8	17	3.30	22.5
3	3.205	21.1	18	3.285	21.9
4	3.18	20.6	19	3.19	20.8
5	3.215	20.0	20	3.185	20.0
6	3.24	20.3	21	3.20	20.6
7	3.25	20.3	22	3.215	20.1
8	3.24	20.6	23	3.235	20.6
9	3.235	21.9	24	3.235	20.6
10	3.24	22.2	25	3.215	21.1
11	3.22	21.7	26	3.21	20.8
12	3.24	22.2	27	3.205	21.1
13	3.24	22.2	28	3.21	21.4
14	3.24	22.2	29	3.21	21.4
15	3.21	21.7	30	3.04	21.7
			31	3.065	21.7

Fish Commission from their collections off the Fish Commission Pier and is given for comparison with records from wharf pilings and also with those from open water.

The vertical distribution in the wharf piling association is marked. Near the high tide level may be found the *Littorinas*, *Urosalpinx*, *Balanus balanoides* and an occasional *Asterias forbesi*. Nearer the water at low tide are *Mytilus* clusters and *Modiolus modiolus* sheltering *Libinia dubia* and *Lepidonotus*. Below these, normally under water at all times, come *Amaræcium* and *Styela* and other pile dwelling chordates. Here are found the sponges, *Microcione*, *Grantia* and *Cliona* and the hydroids such as *Tubularia* and *Schizotricha*. With all these there is the attendant fauna of worms, *Lepidonotus*, *Harmothoe*, *Sthenelais*, *Nereis pelagica* and *limbata;* the sea slug *Coryphella* and the *Columbella* snails are also abundant. Here also are *Bugula* and the encrusting bryzoans, *Schizoporella*, *Lepralia*, *Membranipora* and the like. Below these are the sea anemones, *Metridium*.

The animals mentioned may be displaced somewhat from the order given but as one looks down the outer piles at Vineyard Haven four distinct bands can easily be recognized: The *Balanus* band well above the low water level; the *Mytilus* band near low water, the *Amaræcium-Tubularia* band which shows as a more brilliantly colored region and finally the dull brown of the *Metridium* band which extends well down toward the bottom of the pilings.

Apart from the obvious relations in the upper portion where independence of water is the controlling factor, the vertical distribution may be in part the effect of light differences particularly on the free swimming larvæ. Grave ('20) has found that *Amaræcium* tadpoles, for example, are first positive but soon become negative to light. In part the position may be a response to gravity for the same tadpoles are at first negative in their reaction to gravity and later become positive. When both light and gravity act as they would in nature, the tendency of the tadpoles to settle to the bottom of the experimental cylinder was most marked and occurred in 85 per cent. of the cases. The banding may also be controlled in part by reactions to pressure and to conditions in the water that could not be detected by the measurements made. On the whole Grave is inclined to attribute the distribution of *Amaræcium* colonies to the effect of gravity during the active, free-swimming life of the tadpoles.

c. Rock Associations.—There are two distinct types of animal associations to be found in the region dominated by rocks. First, there are the animals and plants attached to the rocks and rockweeds or living among those so attached and, second, there are the animals living in the substratum under and sometimes between the rocks. These last are closely similar to the animals of the mud or sand flats near which the rocks are located. No attempt has been made to get water samples exactly characteristic of the second community, since in this work the main attention was focused on the animals of the rocks.

Two animal associations of the rocks proper are easily recognized. On the exposed rocks, where there is little rockweed, the animals are mainly found under the edges of the rocks out of the direct sweep of the waves. In protected regions, the rocks are covered with the rockweeds, *Ascophyllum* and *Fucus*. Here

many of the animals are to be found on the upper surface of the rocks under the protecting rockweed. This association may be designated as the protected rock association or more obviously as the rockweed association.

(1) *Exposed Rock Association.*—The association inhabiting the exposed rocks was much studied at the opening of Northwest Gutter into Buzzards Bay. The rocks are exposed to the full sweep of the waves across the Bay and support a sparse growth of *Ascophyllum* and *Fucus*.

Similar conditions are common along the coast. They were studied in three localities: (1) At the outer point of East Buck Island in Lackey's Bay; this differs only in that submerged vegetation lies closer to the rocks on the shore side and extends around the rocks on the Sound side. The waves from the Sound break freely over these rocks. (2) At Gansett on the point which separates Gansett Bay from Quissett Harbor. The whole bottom nearby is covered with eel-grass while in the immediate vicinity *Sargassum filipendula*, *Ascophyllum* and *Fucus* grow in abundance. These rocks are frequently reached by the direct waves from Buzzards Bay and are themselves practically free of rockweeds. (3) In the region of Southwest Gutter where the rocks are protected from the sweep of the waves but are washed by strong and almost constant tidal currents coming now from the Sound and now from the Bay. The direction of the current makes little difference in the character of the water since in either case it passes through tortuous, shallow passages supporting a large amount of submerged vegetation. While there are many plants nearby, these rocks do not support a large amount of plant life. Water analyses from this association are given in Table V.

The animals most common in the exposed rock association are the sponges, *Microcione* and *Cliona;* the actinians, *Sagartia leucolena* and *luciæ* and *Metridium;* the starfish, *Asterias;* the annelids, *Harmothoe*, *Hydroides*, *Lepræa* and *Lepidonotus;* the bryozoan *Bugula* and various incrusting forms; *Balanus balanoides* and *eburneus*, the barnacles; *Chætopleura*, the chiton; the bivalve molluscs, *Anomia* and *Mytilus;* the snails, *Acmea*, *Littorina litorea*, *Eupleura*, *Purpura* and *Urosalpinx;* and the chordates, *Amaræcium*, which is usually and characteristically

TABLE V.

SHOWING OXYGEN CONTENT, pH, TEMPERATURE AND SALINITY OF WATER FROM THE ANIMAL ASSOCIATION OF THE EXPOSED ROCKS.

Date 1920.	Depth Water.	Tide.	Temp.	pH.		O_2.		Time.	Light.	Salinity.	Coll. No.	Place.
				Bot.	Sur.	Bot.	Sur.					
8.14	2 ft.	Flowing	21	8.1	—	—	—	4:30	Dull	3.04	9	Gutter (N.W.)
8.18	1 ft.	Ebbing almost low	21	8.1	—	3.62		3:50	Dull	—	37	
8.23	1 ft.	Low	20	8.0	—	4.41	—	9:00	Dull	3.04	50	
8.24	3 ft.	Flowing almost low	20	8.0	—	4.95	—	11:10	Bright	2.94	65	
9.3	7 ft.	2/3 in	20	8.0	—	4.25	—	10:00	Bright	2.99	108	
8.25	2 ft.	Low to bay	21 on surface	—	8.2	—	5.45	11:35	Bright	—	79	Gutter (S.W.)
8.25	6 ft.	Low to bay	21 on surface	—	8.2	—	6.54	12:45	Bright	3.01	81	
9.3	6 ft.	Slack	21 S.	—	8.2	—	5.39	2:30	Bright	3.01	116	
8.25	1.5 ft.	Low	22 S.	8.2	—	7.03	—	1:30	Bright	3.04	82	Lackey's Bay
9.3	1 ft.	Ebbing	21	8.2	—	4.16	—	4:40	Bright	3.04	120	
8.30	2 ft.	Low	23	8.3	8.3	8.56	—	2:45	Bright	—	89	Gansett
8.30	2.5 ft.	Flowing	22	8.3	—	8.41	—	3:45	Bright	—	91	
8.30	3 ft.	Flowing	—	—	8.3	—	—	4:10	Bright	—	93	
9.1	6 ft.	Near high	22	8.0	8.0	5.15	—	11:30	Overcast	3.05	96	
9.1	2 ft.	Low	21	8.2	—	6.14	—	3:45	Overcast	3.02	104	

LIST 3. SHOWING ANIMALS COMMONLY FOUND IN THE EXPOSED ROCK ASSOCIATION.

Animals starred may be taken above low tide mark.

PORIFERA
- *Cliona celata*(?)
- *Grantia ciliata*
- *Leucosolena botryoides*
- *Microcione prolifera**

CŒLENTERATA
- *Astrangia danæ*
- *Clava leptostyla*
- *Hydractinia echinata**
- *Metridium dianthus*
- *Sargartia leucolena*
- " *luciæ**
- " *modesta*
- *Sertularia pumila*

PLATYHELMINTHES
- *Stylochus ellipticus*

ECHINODERMA
- *Arbacia punctulata*
- *Asterias forbesi**

ANNELIDA
- *Harmothoe imbricata**
- *Hydroides hexagonus**
- *Lepræa rubra*
- *Lepidonotus squamatus**
- *Nicolea simplex*
- *Polycirrus eximeus*
- *Spirorbis spirorbis**
- *Sabellaria vulgaris**

BRYOZOA
- *Alcyonidium* sp.
- *Bugula turrita**
- *Crisia eburnea**
- *Flustrella hispida*
- *Lepralia pertusa*
- *Membranipora pilosa**
- *Schizoporella unicornis**

CRUSTACEA
- *Amphithoe*
- *Balanus balanoides**
- *Balanus eburneus*
- *Cancer irroratus**
- *Idothea metallica*
- *Idothea baltica**
- *Pagurus longicarpus**
- *Panopeus sayi**
- *Spharoma quadridentatum**

(Under rocks)

MOLLUSCA
- *Chætopleura apiculata*
- *Anomia ephippium**
- *aculeata*
- *Modiolus modiolus**
- *Mytilus edulis**
- *Acmea testudinalis*
- *Bittium alternatum*
- *Cerithiopsis emersonii*
- *Columbella avara*
- *lunata**
- *Coryphella gymnota*
- *Crepidula fornicata*
- *convexa*
- *plana**
- *Eupleura caudata*
- *Lacuna vincta**
- *Littorina litorea**
- *palliata*
- *rudis**
- *Purpura lapillus**
- *Odostomia* sp.
- *Urosalpinx cinereus**

CHORDATA
- *Amaræcium constellatum**
- *Botryllus schlosseri**
- *Didemnum lutarium*
- *Molgula manhattensis*
- *Perophora viridis*
- *Styela partita*

present in small clusters, and *Styela*. A more complete list is given in List 3, which while not exhaustive, does represent the association in an adequate manner. The species starred were taken above low spring tide in collecting on the rocks at Kettle Cove, August 4, 1921.

The chance of differentiation in the vertical distribution is not so great here as on the wharf pilings and, in addition, the spaces between the rocks and under them hold moisture better than in the case of the pilings so that the break at the tide level is less marked. Nevertheless the animals to be found on the rocks vary greatly with the height above mean low tide. Differences found in animal life and in water analyses at different tide levels are given in List 4 and Table VI. The high tide levels were studied on the Northwest Gutter rocks. The tidepool and region below low tide are from data obtained at Gansett. There is no reason to suppose that high tide conditions are different in the two places.

The tidepool was well separated from the water of the Bay. It contained about 6–12 inches of water and was one foot wide by three feet long. Some rockweeds were present but not in the numbers common in a typical rockweed association.

It is possible that the greater acidity combined with the decreased oxygen content of the water at the margin at high tide might cause sensitive larvæ to turn back. However when the waves are running well they would have no power in the matter. It is also possible that the sensitive animals of the exposed rock association are kept out of the tide pools by the great range in acidity which was over twice that found on the nearby rocks below low tide and, as seen in List 4, the animals present are fewer in numbers and in species.

(2) *Protected Rocks or Rockweed Association.*—The best example of the rockweed association to be studied was found in the creek between Southwest Gutter and Hadley Harbor. In this place the rockweeds, *Ascophyllum* and *Fucus*, form a patch about two rods square which reaches half way across the creek. The water ranges from six inches to four feet in depth. Between the rocks on the bottom are small patches of gravelly sand mixed with humus. Large boulders, which extend well out of the water at

TABLE VI.

SHOWING OXYGEN CONTENT, pH, TEMPERATURE AND SALINITY OF WATER OVER DIFFERENT TIDAL LEVELS OF MORE EXPOSED ROCKS.

Date 1920.	Depth of Sample.	Tide.	Temp.	pH.		O_2. Bot.	Light.	Time.	Salinity.	Coll. No.	Place.
				Bottom.	Surface.						
8/16	2 ft.	High	21	7.8	—	3.56	Dull	9:10	—	10	Gutter (N.W.)
				7.9	—	3.72					
8/18	1 ft.	Half	22	7.9	—	3.18	Rainy	9:30	—	24	
8/30	.7–1 ft.	Low	24	8.4	—	8.32	Bright	3:00	—	90	Tide pool Gansett
8/30	1.25 ft.	Flowing	24	8.4	—	8.02	Bright	4:00	—	92	
8/30	1.5 ft.	Flowing	23	8.4	—	8.02	Sunny	4:20	—	94	
9/1	3 ft.	Ebbing	22	7.7	—	5.15	Overcast	11:40	3.05	97	
9/1	.7 ft.	Flowing	22	8.0	—	5.94	Sunny	4:00	3.06	105	
8/30	2 ft.	Low	23	8.3	8.3	8.56	Bright	2:45	—	89	Below low tide Gansett
8/30	2.5 ft.	Flowing	22	8.3	—	8.41	Bright	3:45	—	91	
8/30	3 ft.	Flowing	—	—	8.3	—	Bright	4:10		93	
9/1	6 ft.	Near high	22	8.0	8.0	5.15	Overcast	11:30	3.05	96	
9/1	2 ft.	Low	21	8.2	—	6.14	Overcast	3:45	3.02	104	

LIST 4. SHOWING ANIMALS FOUND AT DIFFERENT TIDE LEVELS ON MORE EXPOSED ROCKS.

A. At extreme high tide; NW. Gutter rocks.

Orchestia agilis.

Talorchestia longicornis.

B. At Half Tide; Same Place.

CŒLENTERATA:

Sertularia pumila, much.

CRUSTACEA

Balanus balanoides, very abundant.

MOLLUSCA:

Mytilus edulis, several, small.

Littorina litorea, very many.

rudis, several.

palliata, some on *Ascophyllum*.

C. Tide Pool among Rocks, Gansett.	*D. Below Low Tide, Gansett.*
PORIFERA	
Cliona celata. (?)	Ten times as much as in *C.*
Microcione prolifera, some.	Much, more than in *C.*
	Leucosolenia botryoides, sev. colonies.
	Grantia ciliata.
CŒLENTERATA:	
Sagartia leucolena, few	Several
	Astrangia danæ, sev. colonies
	Metridium dianthus, several.
	Sertularia pumila.
BRYOZOA:	
Bugula turrita	More here.
	Crissia eburnia, 1 colony.
ANNELIDA:	
Harmothoe imbricata, several.	Several, more than in *C.*
Hydroides hexagonus	Many more than in *C.*
Lepræa rubra, few.	Many.
Lepidonotus squamatus	About same as *C.*
Spirorbis spirorbis.	
CRUSTACEA:	
Balanus balanoides, very many	Some
	Gammarus sp. many.
MOLLUSCA:	
Anomia ephippium, several small.	Large ones here.
Acmea testudinalis	More than in *C.*
Cerithiopsis emersonii	None.
Littorina litorea, very abundant.	Fewer than in *C.*
Urosalpinx cinereus	Many more than in *C.*
	Chætopleura apiculata, few large.
	Anomia aculeata, several small.
	Modiolus modiolus, few.
	Crepidula plana, few.
	Littorina rudis, few.
CHORDATA:	
Stylela partita	Few in both.
	Amaræcium constellatum, much.

low tide, support masses of the rockweeds. The water here is constantly changed by the strong tidal current.

A similar situation, except for the tidal current, was examined at the inshore end of Gansett Bay. The region there is in the form of a triangle with the shore for the long base and with the apex made by a large boulder lying about two rods off shore at low tide.

A partial list of the animals to be found in this association, divided according to strata, is given in list 5. As might be expected, animals usually found only at or near low tide, occur here well above low tide in some abundance on account of the protection furnished and the water held by the rockweeds.

LIST 5. SHOWING REPRESENTATIVE ANIMALS OF THE ROCKWEED ASSOCIATION BY STRATA.

A. Animals on or Among the Rockweed when Left Exposed by the Tide.

CŒLENTERATA:
Clava leptostyla,
Obelia geniculata,
Sertularia pumila,
Sagartia luciæ.

ECHINODERMA:
Asterias forbesi.

BRYOZOA:
Alconidium sp.?,
Bugula turrita,
Flustrella hispida.

ARTHROPODA:
Amphithoe rubricata,
Caprella geometrica,
Balanus balanoides,
Anoplodactylus lentus,
Limulus polyphemus.

MOLLUSCA:
Mytilus edulis,
Littorina litorea,
Littorina palliata,
Columbella avara,
Columbella lunata.

B. Animals from the Rocks Below the Rockweed Stratum from First Six Rocks Examined.

PORIFERA:
Cliona celata, (?)
Microcione prolifera.

CŒLENTERATA:
Sagartia leucolena.

ECHINODERMA:
Asterias forbesi.

BRYOZOA:
Lepralia pertusa,
Membranipora pilosa.
Schizoporella unicornis.

ANNELIDA:
Harmothoe imbricata,
Lepidonotus squamatus,
Hydroides hexagonus,
Polycirrus eximeus.

ARTHROPODA:
Cancer irroratus.

MOLLUSCA:
Mytilus edylis.

CHORDATA:
Styela partita.

C. Animals Found in Brief Examination on Surface of Substratum.

CRUSTACEA:

Cancer irroratus,
Libinia dubia carrying the sponge, *Cliona celata,* (?)
Pagurus longicarpus carrying the hydroid, *Hydractinia echinata,*
Panopeus sayi.

GASTEROPODA:

Littorina litorea, very numerous.

D. Animals Found in Sampling the Substratum. (*Three spadesful were dug.*)

PLATYHELMINTHES:

Lineus ochræus.

MOLLUSCA:

Cumingia tellinoides,
Nassa trivittata.

ANNELIDA:

Clymenella torquata,
Lepræa rubra,
Lumbrinereis tenuis,
Nereis limbata,
Pectinaria gouldii.

Water analyses for this association are shown in Table VII. The table includes the last six items from the preceding table, since the conditions described in those collections are as characteristic of the one as of the other. A discussion of the water analyses for this and the other associations of the eroding shore series is reserved to a later section.

Here this series logically ends so long as the shores remain under erosion with a gradual wearing away of the land to expose more rocks, which would result in the association of the exposed rocks moving gradually forward as erosion proceeds. In case the shore line should remain stationary for sufficient time, the rocks might be worn away to sand and this association might conceivably pass gradually into that of the sand bar which will be considered in the next section. On the other hand if the configuration of the land changes so that currents no longer cause erosion, but deposition sets in, then in the region of the present rock associations one may find sand deposited and the sand bar association might be reached by that route. If the region becomes still more quiet, mud might be deposited and the rock association would then pass to the *Mya* association and with further deposition, pass into the *Uca* or *Melampus* stage. The physical factors correlated with these associations will be given on a later page and anyone interested in completing this series on either of these possibilities, can readily do so.

TABLE VII.

SHOWING OXYGEN CONTENT, TEMPERATURE. pH AND SALINITY OF THE ROCKWEED ASSOCIATION.

Date 1920.	Depth of Sample.	Tide.	Temp.	pH.		O_2		Time.	Light.	Salinity.	Coll. No.
				Bot.	Sur.	Bot.	Sur.				
						Gansett.					
8/30	2 ft.	Low	23	8.3	8.3	8.56	—	2:45	Bright	—	89
8/30	2.5 ft.	Flowing	22	8.3	—	8.41	—	3:45	Bright	—	91
8/30	3 ft.	Flowing	—	—	8.3	—	—	4:10	Bright	—	93
9/1	6 ft.	Near high	22	8.0	8.0	5.15	—	11:30	Overcast	3.05	96
9/1	1 ft.	Near low	23	8.0	—	5.35	—	2:45	Bright	2.97	103
9/1	2 ft.	Low	21	8.2	—	6.14	—	3:45	Overcast	3.02	104
						S. W. Gutter Creek.					
9/3	2–2.5 ft.	Slack	19	8.0	—	4.75	4.75	2:15	Bright	3.01	115
8/25	1–1.5 ft.	Low to Bay	21	8.0+	8.0+	4.75	5.35	9:10	Bright	2.98	77

2. *Associations of Depositing Shores.*

Notwithstanding the slight amplitude of tides in the Woods Hole region, there are a number of fairly extensive tidal flats which furnish the basis for the associations of the depositing shores. The best of these near the Laboratory is the flat opening off Northwest Gutter just before it enters Buzzards Bay. The majority of collections to be reported were made at this place. Verification studies were carried on in Lackey's Bay, at Gansett, and in Southwest Gutter Creek.

The different animal habitats to be found on the flats grade slowly from one to another so that it becomes impossible to get hard and fast limiting lines. This is true even of the more extensive flats, those at North Falmouth for example, but it is particularly marked in regions such as Gansett where the water deepens fairly rapidly, leaving only narrow zones along the margin. Similar jumbling of habitats is to be found in the salt water creeks of Hadley Harbor and is more characteristic of the Woods Hole coasts than are the more gradual transitions found on the flats proper.

Theoretically the youngest stage in this series is that shown in (*a*) the association of the open water. The conditions in such positions have already been discussed so we shall proceed immediately to the associations of the flats.

b. The Sand Bar Association.—In this region tidal flats are typically separated from the open water by sand bars which may be much exposed at low spring tides, or just covered at low neap tides. The outer part of the bar is relatively pure sand which gradually becomes mixed with humus as one moves back on the flats. The characteristic animals of such an association are given in list 6.

In places practically pure cultures of *Scoloplos fragilis* occur in the sand and if an animal name for the association is desired it might well be called the *Scoloplos fragilis* association.

Where the sand bar extends out to the margin one finds the expected evidences of vertical distribution depending on tide level. At the upper tidal limit congregating under the eel grass occur great numbers of the beach flea, *Orchestia agilis;* burrowing in the sand are the *Talorchestia longicornis* and locally, *Hippa talpoida.*

LIST 6. CHARACTERISTIC ANIMALS OF THE SAND BAR ASSOCIATION.

CŒLENTERATA:
Hydractinia echinata on shells occupied by *P. longicarpus*.

NEMERTINI:
Cerebratulus lacteus,
Micruri leidyi.

ECHINODERMA:
Leptosynapta inhærans.

ANNELIDA:
Clymenella torquata,
Diopatra cuprea,
Phyllodoce sp.,
Scoloplos fragilis,
Scoloplos robustus.

ARTHROPODA:
Crangon vulgaris,
Ovalipes ocellatus,
Pagurus longicarpus,
Limulus polyphemus.

MOLLUSCA:
Crepidula convexa, on hermit crab shells,
Crepidula plana, on hermit crab shells,
Ensis directus,
Nassa trivittata,
Natica duplicata, with egg collars.

CHORDATA:
Dolichoglossus kowalevskyi.

The conditions of the water over this association are shown in Table VIII. The last item in the table was from Blind Gutter

TABLE VIII.

SHOWING TEMPERATURE, SALINITY, OXYGEN CONTENT AND pH OF SEA WATER OVER THE SAND BAR ASSOCIATION.

Date 1920.	Time.	Depth Water in Ft.	Tide.	Temp. °C.	pH.	O_2 in c.c. per L.	Light.	Salinity.	Collection Number.
8/14	3:15	1.0	Low	24.5	8.25	—	Dull	3.10	4
8/16	11:30	6.0	High	22.0	8.0	—	Dull	—	13
8/18	2:20	1.5	Ebbing	22.0	8.1	—	Rainy	—	30
	4:00	0.5	Low	21.0	8.1	—	Rainy	—	38
8/23	9:35	0.75	Low	20.0	7.6	3.91	Dull	—	51
8/24	11:15	0.5	Flowing	20.0	8.0	4.63	Bright	2.99	66
9/3	10:30	5.0	Flowing	20.0	8.0	3.95	Sunny	2.99	109
9/3	4:30	1.25	Ebbing	20.0	8.2	4.16	Sunny	3.02	119[1]

Bar. The others are from Northwest Gutter Bar. With the exception of one reading, made in triplicate, the pH ranges from 8.0 to 8.25. In this respect it approaches open water. The observed range is greater than that of the nearby rocks. The salinity is similar to that of the rocks and less than that of the open water. The oxygen content resembles that of exposed rocks where rockweeds are absent. The temperature range is greater than in any other association so far studied and the

[1] Blind Gutter Bar.

temperature at the upper surface of the sand when fully exposed to the afternoon sun must run much higher than the recorded 24.5° C. observed for the water under these conditions. The pH at Blind Gutter shows the effect of the neighboring vegetation which lies on both sides of this bar.

c. Muddy Sand Association.—The association of muddy sand shades insensibly into the preceding animal community on its outer side. On its inner side it includes the short eel grass (*Zosteria marina*) which extends well out on the sand and then gradually passes into the eel grass and muck association. The most characteristic animal of the association is the sipunculid worm, *Phascolosoma gouldii* and the association might well be called the *Phascolosoma* association. Much of the muddy sand may be exposed at extreme low tide.

This community was most extensively studied at Northwest Gutter, but verification studies were run at other points. Common animals of the association are given in list 7 but the animals shown in the preceding list are also found here.

LIST 7. ANIMALS EASILY FOUND IN THE MUDDY SAND OR *Phascolosoma* ASSOCIATION.

(See also List 6.)

CŒLENTERATA
Hydractinia echinata,
Sagartia luciæ.

ANNELIDA
Arabella opalina,
Clymenella torquata,
Drilonereis longa,
Glycera americana,
dibranchiata,
Lumbrinereis tenuis,
Nereis limbata,
Nereis virens,
Pectinaria gouldii,
Phascolosoma gouldii,
Phyllodoce catenula.

MOLLUSCA
Crepidula convexa,
Lacuna vincta,
Lævicardium mortoni
Littorina litorea,
Mya arenaria,
Nassa obsoleta,
Venus mercenaria.

ARTHROPODA
Carcinides mænas,
Heteromysis formosa.
Libinia dubia,
Limulus polyphemus,
Palæmonetes vulgaris,
Virbius zostericola.

CHORDATA
Dolichoglossus.

The analyses of water over the muddy sand association (Table IX.) show an increase in range in all four factors considered when compared with the conditions found on the sand bar. The majority of these samples are from the edge of the short

eel grass. The effect of the eel grass on oxygen content and on pH is noticeable although not so extreme as will be found later. These effects are the expected result of photosynthesis.

TABLE IX.

SHOWING ANALYSES OF THE WATER TAKEN OVER THE MUDDY SAND OR *Phascolosoma* ASSOCIATION.

Date 1920.	Time.	Depth Water in Ft.	Tide.	Temp. ° C.	pH.		O_2.		Salinity.	Light.	Coll.
					Bot.	Sur.	Bot.	Sur.			
				Northwest Gutter.							
8/14	2:10	.25 −.5	Low	25.5	8.45	—	10.39	—	3.10	Dull	1
	4:00	.08	Low	27.0	8.5	—	—	—	—	Dull	1′
	4:05	.5	Flowing	26.0	8.4	—	—	—	—	Dull	6
	4:30	.33	Flowing	27.0	8.45	—	—	—	—	Dull	8
8/16	3:55	1.5	Ebbing	22.0	8.1	—	5.30	—	—	Duller	15
8/18	10:05	4.0	Flowing	22.0	7.9+	8.0−	4.21	—	—	Rainy	25
	2:30	2.0	Ebbing	22.0	8.1	8.1	—	—	—	Rainy	31
	3:45	0.5	Ebbing	—	—	—	4.76	—	—	Rainy	36
8/23	10:00	1.0	Flowing	—	7.8	—	4.2	—	3.04	Dull	52
	1:15	3.0	Flowing	—	8.0−	8.0−	4.75	—	—	Sunny	58
8/24	2:15	2.5	Flowing	21.0	8.0+	8.0+	5.05	5.15	—	Sunny	73
9/3	12:50	5.0	High	21.0[1]	8.1	8.1	4.71	4.63	3.04[1]	Bright	113
				Southwest Gutter Creek.							
8/25	10:20	.08	Low	21	7.7	—	—	—	—	Bright	78
	10:20	.67	Low	21	8.0	—	5.25	—	2.97	Bright	78
	12:10	.75	Low	—	8.0	—	5.20	—	—	Bright	80
				Gansett.							
8/31	1:45	1.0	Ebbing	23	8.2	—	7.63	—	2.97	Sunny	98
9/1	1:15	3.0	Half	21[2]	8.2	8.0	7.08	6.19	2.96	Bright	101
	4:21	1.0	Flowing	23.5	8.4	—	8.61	—	—	Bright	106

d. Eel Grass and Muck Associations.—The associations of the eel grass and muck lie between the last discussed habitat and a region about a rod from the shore line of the type of flats under discussion. There at a depth of about a foot at low tide, the eel grass ends and the marginal muck association begins. Two major recognizable associations occupy this region: that characterized by the bivalve, *Cumingia tellinoides*, which may be

[1] Same at surface.

[2] 23 at surface.

called for convenience the *Cumingia* association and in deeper water and deeper muck, the region characterized by the annelid, *Scoloplos acutus*, which may give its name to this association.

On account of lack of time no water samples were taken over the *Cumingia grounds*. Enough collecting to yield 25 *Cumingia*, gave the following associates:

Annelida: *Polycirrus eximeus*, *Trophonia affinis*, *Amphitrite ornata*, *Glycera americana* and *Maldane elongata*.

Crustacea: *Panopeus sayi*.

Mollusca: *Tellina tenera*, *Solemia velum*, *Nucula proxima*, *Venus mercenaria*, *Lævicardium mortoni*.

Associated with these one usually finds the burrowing anemone, *Edwardsia elegans;* the swimming annelid, *Podarka obscura;* the shrimps: *Palæmonetes*, *Crangon*, and *Hippolyte;* and the green crab, *Carcinides*.

In both Northwest and Blind Gutters the *Scoloplos acutus* association occupies several acres. At Gansett, the whole center of the bay supports a dense growth of eel grass and from general appearances, I should judge that it would belong to this association but it comes out into shallow water only in a relatively narrow zone and there some of the typical animals, *Thyone briareus*, for example, were not found.

LIST 8: SHOWING THE COMMON ANIMALS FOUND ON, AMONG, AND AT THE ROOTS OF EEL GRASS IN THE CENTER OF NW. AND BLIND GUTTER FLATS.

A. ON EEL GRASS.

COELENTERATA:
Sagartia luciæ (frequently many).

BRYOZOA:
Bugula turrita (much).
Schizoporella unicornis (some).

GASTEROPODA:
Bittium alternatum (many).
Crepidula convexa (several).
Crepidula fornicata (few).
Littorina rudis (few).
Littorina litorea (many).
Littorina palliata (few).

CHORDATA:
Molgula manhattensis (very few).
Botryllus schlosseri (little).

B. AMONG EEL GRASS.

ANNELIDA:
Podarka obscura (frequently abundant).

CRUSTACEA:
Virbius zostericola (very many).

MOLLUSCA:
Pecten irradians (many).

C. IN MUCK AT ROOTS.

ECHINODERMA:
Thyone briareus (frequently abundant).

ANNELIDA:
Scoloplos acutus (many).

This association is in the region of tall eel grass which at high tide floats erect, allowing light to penetrate to the bottom. As the tide recedes, the grass falls over and finally at low tide forms dense mats which effectively shade the bottom except in queer open spaces where for some reason the eel grass fails to grow.

The eel grass supports a considerable fauna and flora. Davis (1911) lists 42 species of plants known to occur as epiphytes upon it in the more open situations. The number of animals found in the type of region under discussion is restricted. List 8 shows those found in Northwest and Blind Gutters in this association. The animals listed were collected in about three times the collecting time that gave the *Cumingia* list.

Above the mat of living eel grass at low tide, the temperature runs up as high as 32 degrees C. on a hot afternoon. Just below the matted eel grass, six inches from the water surface the temperature was 27, while at the bottom the thermometer registered 24 degrees. Thus there is a temperature gradient here of eight degrees in 30 inches.

Similar gradients of other environmental factors are present. Thus the oxygen content of the water at the bottom just above the *Thyone* and *S. acutus*, may fall as low as to give a mere trace with the Winkler method, when 24 inches higher, just below the eel grass mat, it was found to be 10.22 c.c. per liter and six inches higher, at the surface, 12.97 c.c. per liter. This makes a total gradient of 12.97 c.c. per liter in 30 inches. The pH gradient was found to be wholly similar: 7.3 at the bottom, 8.5, below and 9.0 above the eel grass matting.[1] These results are the natural concomitants of rapid photosynthesis at the surface of quiet water overlying thick muck.

The greater density was found at the bottom, but when the density was corrected for temperature the determinations showed a higher percentage of salinity at the surface. These and other details are shown in Table X. Particular attention is called to the wide range of variation in the different factors analyzed for this association. In the table, collections 99 and 102 are from

[1] Under laboratory conditions Atkins ('22) reports that sea water may come to have a pH of 9.77 when jars containing *Ulva* are exposed to sunlight.

TABLE X.

SHOWING THE TEMPERATURE, OXYGEN CONTENT, SALINITY AND pH OF THE WATER OVER THE *Scoloplos acutus* ASSOCIATION.

Date 1920.	Time.	Depth in Ft.	Tide.	Temp. ° C.	pH.		O_2.		Salinity.	Light.	Coll.
					Bot.	Sur.	Bot.	Sur.			
8/14	2:35	.25 −.5	Low	25.5	—	8.45	—	—	—	Dull	2
	3:00	.25 −.5	Low	25.0	8.25	—	—	—	—	Dull	3
	4:00	.25 −.5	Low	26.0	—	8.4	—	—	—	Dull	3′
	3:30	.33	Low	26.5	—	8.45	—	—	—	Dull	5
8/16	1:30	1.25	Ebbing	22.0	8.2	—	—	—	—	Duller	16
	2:10	1.0	Ebbing	23.0	7.9	—	—	—	—	Duller	18
	3:00	0.67	Ebbing	—	7.85	—	—	—	—	Duller	20
8/18	11:00	4.5	High	22.0	8.0	8.0	1.96	—	—	Rain	26
	2:45	1.6	Ebbing	—	8.0	8.2	—	—	—	Bright	32
8/23	10:25	1.0	Flowing	20.0	7.85	8.0	2.37	—	—	Dull	53
	1:30	3.0	Flowing	23.0	—	8.4	7.03	7.81	—	Sunny	58′
	2:00	3.0	Flowing	—	—	8.3	—	—	—	Sunny	59
8/24	9:55	0.75	Low	20.5	7.8 7.7	8.6 − 8.6 −	4.9	8.66	3.02	Sunny	63
	11:30	1.25	Flowing	24.0S	8.3	8.6 −	5.69	9.9	—	Sunny	67
	1:30	2.0	Flowing	25.0S 24.0B	8.2	8.5	4.65	8.91	—	Sunny	72
	2:20	2.5	Flowing	23.5S	8.3 +	8.3	5.54	5.31	—	Sunny	74
	2:50	3.0	Flowing	26.0S	8.35	8.7	9.51	10.7	—	Sunny	75′
9/3	11:50	6.0	High	18.0B 20.0S	8.0	8.1	5.88	5.31	2.98B 3.01 S	Bright	112
8/31	2:30	2.5	Ebbing	22.5B 26.0S	7.8	8.6	3.26	10.6	3.01	Sunny	99
9/1	2:00	3.0	Ebbing	22.0B 22.0S			2.28	7.68	2.99	Bright	102
8/25	2:10	2.5	Flowing	24.0B 32.0S	7.3	9.0	Tr.	12.97	2.88	Sunny	83
	3:05	2.5	Flowing	27.0M	8.5M		10.79M		—	Sunny	83′
9/3	3:40	2.5	Ebbing	20.0B 24.0S	7.8	9.0 −	4.25	10.8	3.02B 3.11 S	Bright	118
8/14	4:15	0.25	Low	26.0	8.0	—	—	—	—	Dull	7
8/18	2:00	3.5	Ebbing	22.0	7.7 +	—	2.43	—	—	Dull	29
8/23	12:00	1.5	Flowing	20.0*b*	7.6	7.9	4.46	4.6	3.02	Bright	56
	1:00	2.1	Flowing	20.0	7.9	7.9	—	—	—	Bright	57
8/24	10:50	0.67	Low	22.0	8.1	8.1	4.95	—	—	Bright	64
9/3	1:00	4.5	High	21.0*c*	8.0	8.1	4.32	4.84	3.01*c*	Bright	114

Collections marked "S" are from the surface; "B," are from the bottom; "M" are from six inches below the surface. Collections not otherwise labeled are from the bottom.

a. Collection No. 75, although taken after No. 74, was from further inshore and represents an earlier stage in the rising tide.

b. 21 at surface.

c. Same at surface.

Gansett; 83 and 118 are from Blind Gutter Flats. The others are from NW. Gutter Flats.

One open space in the eel grass, similar to those occurring scattered over the flats, except that it is larger and occurs near the margin, is to be found at NW. Gutter where a gravel spit extends from Uncatena Island partially across the creek leading to Hadley Harbor. On the Hadley Harbor side of the spit is a space covering some 2–3 square rods close up in the angle made by the gravel with the shore. The almost bottomless muck is covered over by a thick layer of old eel grass which acts as a very effective matting over the soft ooze below. Such eel grass is very resistant and decays slowly. The main tidal current flows past the edge of this eddy and thus prevents conditions from becoming as extreme as they would otherwise.

In addition to the numerous mud snails (*Nassa obsoleta*), one may find here: a few hermit crabs (*P. longicarpus*) carrying *Hydractinia* and the snail, *Crepidula convexa*. In places the common *Littorina litorea*, almost equals the mud snails in numbers and in other nearby regions only the latter are found. Some *Libinia dubia* are also on the surface while under the matting one finds nothing save a few *Scoloplos fragilis*.

The analytical data collected from this locality is shown in the latter part of Table X, commencing with collection No. 7. In many respects the conditions in this particular location resemble those of the *Thyone* association and seem to present a transition stage between the two associations. This will be discussed in detail in the last section.

e. Marginal Muck (Thyone) Association.—*Thyone* occurs in the preceding association as well as here, but since they are easily the most conspicuous animals in this environment and there are at least as many of them here as among the eel grass, and they may be absent in typical *S. acutus* conditions, the name is entirely appropriate.

The marginal muck association inhabits the region between the edge of the eel grass and low tide and overlaps both the preceding and the following associations. The eel grass on muddy shores usually begins to grow where the water is from one to two feet deep at low tide. This leaves a space from one to two rods wide on the inner side of Northwest and Blind Gutter Flats, bare of

vegetation and with a bottom of soft muck some eight inches or more deep. The *Thyone* bury themselves in this muck, leaving only the tentacles and cloacal opening exposed. They are frequently numerous and may be seen over considerable extent with one or more for every square yard.

Associated with *Thyone briareus*, in such locations are: a few of the worms, *Clymenella;* many *Lumbrinereis tenuis*, and the clam-worm, *Nereis virens*.

Of the crustacea, *Carcinides mœnas*, the green crab, is most conspicuous and may frequently be seen running along the bottom, dodging in and out of the eel grass. The ever-present small hermit crabs, *P. longicarpus*, with their usual commensals, are present in some abundance together with the shrimp, *Crangon vulgaris*. The mud crab, *Panopeus*, is also found.

The molluscs are represented by *Modiolus demissus*, near the edge, where *Mya* and *Venus* also occur. There are also a few strings of *Mytilus edulis* and some rolls of *Crepidula fornicata* to be found. Mud snails, *N. obsoleta*, are also present.

TABLE XI.

SHOWING THE RESULTS OF ANALYSES OF THE WATER OVER THE *Thyone* ASSOCIATION.

All but the last two items are from NW. Gutter Flats; those are from Blind Gutter Flats.

Date 1920.	Time.	Depth in ft.	Tide.	Temp. ° C.	pH.		Oxygen.		Salinity.	Light.	Coll. No.
					Bot.	Sur.	Bot.	Sur.			
8/16	1:45	1.0	Ebbing	22	7.8	—	4.08	—	—	Dull	17
	2:45	0.67	Ebbing	22	7.8	7.8	—	—	—	Dull	19
8/18	12:30	4.2	Ebbing	22	—	8.0	—	—	—	Dull	27
	3:15	1.0	Ebbing	22	7.4	—	4.45	—	2.22	Rain	34
8/23	11:00	1.0	Flowing	20	7.9	7.9	4.53	—	3.01	Dull	54
	11:30	1.5	Flowing	20.5	—	—	—	—	3.01	Dull	55
	2:00	3.0	Flowing	20.5	8.2	8.2	6.20	8.37	—	Bright	59
5/24	9:15	1.0	Ebbing	21	7.8	7.8	3.96	—	3.04	Bright	62
	12:30	1.0	Flowing	24	8.0	—	—	—	—	Bright	69
	3:15	3.0	Flowing	26	—	8.5	—	—	—	Bright	76
9/3	11:30	4.5	High	17B 20S	7.4	8.2	3.23	5.51	2.88B 3.02 S	Bright	110
8/25	3:45	1.0	Flowing	28	8.2	—	6.79	—	3.10	Bright	84
9/3	3:20	1.6	Ebbing	22	8.0	—	5.31	—	3.08	Bright	117

B, collection from bottom; S, collection from surface.

Except for salinity, the water over the marginal muck association shows much less range in variation than in the *S. acutus* association. Thus the recorded temperature range is 11° C. against 15°; the pH range, 0.8 *vs.* 1.7; the oxygen, 5.24 c.c. per liter against 12.97. These are the natural results of the lack of green plants in this association. On the other hand a careful (laboratory) determination of salinity, made just after a heavy shower that was one of a series running through a whole morning, showed the effects of fresh water drainage from a nearby swale by recording a salinity of 2.22 per cent. It is probable that this lessened density extended into typical *Scoloplos acutus* territory, though in a less marked form, but no tests have been made there under these conditions. Dilution after a really heavy rain would be much greater. The results from analyses of water over the *Thyone* beds are shown in Table XI.

f. The Intertidal Associations.—In this area the flats extend back to old shore lines where the rocks characteristic of shores are being gradually covered by mud accumulations; these are the typical mud flats which I have been describing. These margins, rising more or less steeply from the water, are the home of the intertidal associations. Most obviously there are two of these: that of the animals near the low tide level, and that near high tide. The former is dominated by *Mya* and is best understood if called the marginal *Mya* association; the latter association depends on location for its typical animals. That most studied has been the *Melampus* association.

(1) *The Mya Association.*—In the localities studied for this report, the *Mya* association is best represented along the west shore of Northwest Gutter Flats. The rocks there are an extension of those of the exposed rock association, but since they are located in the back part of the flats, mud has been deposited around them until in many places they are almost entirely covered up to the mid-tidal region. Here from well below low tide to about mid-tide the siphons of small *Mya* [1] are so numerous as to appear like stippled spots against the mud background. In the lower part, the larger siphons of *Venus* give variety to the stippling. If one try to dig up the clams, he encounters the buried rocks within a few inches of surface.

[1] Mr. G. M. Gray informs me that he has never taken *Mya* in pure muck.

Other animals to be found here are: *Natica duplicata*, *Nereis virens*, *Polycirrus eximeus*, burrowing in the mud; *Nassa obsoleta* and the hermit crab, *P. longicarpus*, with its commensals, *Hydractinia* and *Crepidula convexa*, on the bottom, retreating as the tide ebbs; and *Ostræa virginica* growing occasionally on the rocks.

TABLE XII.

SHOWING THE RESULTS OF ANALYSES OF THE WATER OVER THE *Mya* ASSOCIATION.

Date 1920.	Depth in Inches.	Tide.	Temp. ° C.	pH.	Oxygen c.c. per Liter.	Light.	Salinity %.	Time.	Collection Number.
8/16	1	Ebbing	28.0	7.5	—	Dull	—	3:15	21
8/18	1	Ebbing	22.0	7.1	—	Dull	2.22	3:00	23
8/23	1	Flowing	20.0	7.9	—	Dull	—	11:00	54
	1	Flowing	20.5	8.2+	—	Bright	3.01	2:30	60
							3.01		
8/24	1	Ebbing	21.5	7.8	3.72	Bright	—	9:00	61
	1	Flowing	27.0	7.6	—	Bright	3.04	12:15	68
	1	Flowing	28.0	8.0	—	Bright	3.10	1:25	70
9/3	36	High	19.0	7.8	4.86	Bright	3.04	11:45	111

The temperature of the water in this association runs much higher than on the rocks; 28 degrees C. was recorded. The exposed mud at low tide must run still higher. Few oxygen tests were made here, but they showed, as was expected, that there is a good supply of oxygen in the water. In the upper reaches, at least, the water does not cover the mud long enough to lose much of its supply which came in with the high tide. Under low tide conditions the mud must contain almost no oxygen at all. The pH may be markedly lower than on the other associations, correlated with the fact that the muck is acid. The observed salinity is the same as for the marginal muck association but it probably runs lower on occasion, from the drainage after rains.

TABLE XIII.

SHOWING THE TEMPERATURE, OXYGEN TENSION, AND pH OF THE *Melampus* ASSOCIATION.

Date 1920.	Depth in Inches.	Tide.	Temp. ° C.	pH.	Oxygen c.c. per Liter.	Light.	Salinity.	Time.	Coll. No.
8/16	1	Ebbing	23	7.4	1.96	Dull	—	12:00	14
8/18	1	Ebbing	22	7.2	1.81	Raining	—	1:30	28

(2) *High Mud Shores* (*Melampus*) *Association.*—The last type of habitat in the series comes with the further deposition of organic mud. Under these conditions the *Mya* association would gradually be raised above low tide level and finally above mid tide level. Marsh grasses would come in and in place of the association dominated by *Mya* there would be one dominated in places by the fiddler crabs (*Uca*) and in others by the snail *Melampus lineatus*. The situations studied have had more of the latter than the former.

The *Melampus* grounds are well illustrated in the Uncatena shore of Northwest Gutter from near the bridge to the gravel spit marking the eastern side of the passage to the Bay and at various places along the other gutter creeks, especially near the rockweed association already located.

The substratum is a peaty mixture of muck and roots which is covered only at high tide and then by only a few inches to a foot or so of water. In the lower parts the mussel *Modiolus demissus* is present sometimes in abundance. At the upper side the land insects, such as the carabid beetles, are plentiful, while Thysanura are abundant over much of the region at low tide. The ground is moist at all times on account of the spongy character of the substratum and the protection furnished by marsh grasses.

Too few analyses of water of this region have been made but the low pH and accompanying low oxygen content of the water as it leaves the flat when the tide ebbs, is significant. When this water flows over the *Melampus* grounds, it would have a pH of about 8.0 and an oxygen tension of some 4.00 c.c. per L. The locality most studied would be covered with water about six hours of the twenty-four. The salinity must vary from about 3.00 per cent. at high tide to practically fresh water when low tide coincides with a heavy rain.

IV. Summary of Data.

There are two types of data which one desires concerning the environmental complex of animals: First, what are the average conditions during the period when the divisions between habitats are most pronounced? And second, what extremes are to be

found within a given association? The available data on these points for the months of August and early September, will be presented by tables for the two series studied.

a. Rocky Eroding Shores.—The average conditions in the eroding shore series when conditions are most acute, are shown in Table XIV. This series is composed of the associations of

TABLE XIV.

ERODING SHORE SERIES.

Showing average salinity, oxygen content, temperature, and pH of different animal associations as found in collections from the bottom at low tide except for salinity where low and mid-tide data are averaged. The last two associations are added for comparative purposes.

Ordinal ranking is based upon variation from conditions known to occur in open water.

Association.	Salinity.			O_2 c.c. per L.			Temperature.			pH.			Sum of Ranks.
	No. Rec.	Ave. ‰	Rank.	No. Rec.	Ave.	Rank.	No. Rec.	Ave. ° C.	Rank.	No. Rec.	Ave.	Rank.	
Open	12	3.12	1	12	5.17	1	10	21.1	2	15	8.0	1.5	5.5
Wharf pilings	4	3.05	2	12	4.72	2	11	20.0	1	13	8.0	1.5	6.5
Exposed rocks	6	3.02	3	8	5.91	3	11	21.4	3	9	8.16	4	13
Rockweed	4	2.99	4	6	6.33	4	6	21.5	4	6	8.13	3	15
Mya	5	2.88	5	1	3.72	5	7	24.0	6	7	7.7	5	21
Melampus	0	—	6[1]	2	1.88	6	2	22.5	5	2	7.3	6	23

the open water, wharf pilings, exposed rocks, and rockweeds growing on protected rocks. Data from the intertidal associations at the back of mud flats are added for comparisons.

The average salinity at low and mid-tides decrease in the order given. The average low tide temperatures increase in the order given from the wharf pilings but these, contrary to expectation, are lower than the open water. The average oxygen tension varies from that found in the open water by amounts which likewise arrange the series in the order given. Thus the wharf pilings gave an average of 4.72 c.c. of oxygen per liter which is 0.49 less than the average found in open water; while the exposed rock association with an observed average of 5.1 c.c. per liter is 0.74 c.c. from the open water conditions.

[1] Must range from almost fresh water during rain at low tide to about 3.00 at high tide.

The pH averages the same in the wharf pilings and open water associations. The rockweed association comes next with the association of exposed rocks very near it. The pH values from the exposed rock association is higher than would be expected for the entire coast because only one of the three places in which it was studied was free from the influence of nearby submerged vegetation. Under entirely typical conditions the average pH in this series should likewise arrange the series in the same order as the other factors measured.

The rankings given in the table are based upon the extent of variation from conditions known to be characteristic of open water. The sum of the ordinal ranks, a poor enough method of averaging, shows a gradual increase corresponding to the ecological age of the associations.

The range of these four factors (Table XV.) tends to increase with the age of the association. This is not true of each factor taken separately, nor is the increase in total amounts in regular order, in that the rockweed association on this basis precedes the exposed rock association, when it would be expected to follow it.

In addition to the absolute range the data from these extremes show another set of relations not given in averages, that is the relative position of the extremes. In salinity of the open water the lowest record is fairly high and, while the upper extreme of salinity remains approximately constant, there is a general fall in the lower limit as one passes from open water to the older associations.

In the temperature series the characteristic change is in the matter of the greater maximum in the older associations. With pH, the young associations have practically no change, the older ones have an increased upper limit due to the action of plants, while the oldest ones show a decided decrease in the minimum on account of the acid-giving muck which is deposited in them.

A combination of the rankings based on the departure of average low tide conditions from those known to occur in open water and on amount of variation between observed extremes, places the associations in order of their ecological age, with the exception of the rocks and rockweed associations which are placed together. If in place of an index figure based on amount

of variation of extremes one substitutes the more complex index shown in Table XV., which combines the amount of variation with the location of extremes, the series is arranged by the data given here exactly in order of ecological age.

TABLE XV.

ERODING SHORE SERIES.

Showing range of variations of temperature, oxygen content, salinity, and pH at the stratum most studied in each animal association; all tide stages considered. The last two associations are added for comparative purposes.

Ordinal ranking is based on amount of variation and relative location of extremes.

Association.	Salinity in Per Cent.			Oxygen in c.c. Liter.			Temperature in Degrees C.			pH.			Ranking.		
	Limits.	Range.	Ordinal Rank.	Limits.	Range.	Ordinal Rank.	Limits.	Range.	Ordinal Rank.	Limits.	Range.	Ordinal Rank.	Sum of Ranks.	Combined Ranking.	Final Ranking.
Open.....	3.02			3.93			20			8.0 −					
	3.14	0.12	1	5.43	1.50	1	22	2.0	1.5	8.0 +	0.01	2	5.5	11	1
Wharf pilings.....	2.97			4.06			19			8.0					
	3.13	0.16	2	6.00	1.94	2	21	2.0	1.5	8.0	0.0	1	6.5	13	2
Exposed rocks.....	2.94			3.62			20			8.0					
	3.04	0.10	3	8.56	4.94	4	23	3.0	3	8.3	0.3	3.5	13.5	26.5	3
Rockweed .	2.97			4.75			19			8.0					
	3.02	0.5	4	8.56	3.81	3	23	4.0	4	8.3	0.3	3.5	14.5	29.5	4
Mya.....	2.22			0.0[1]			19			7.1					
	3.10	0.88	5	4.86	4.86	4.5	28	9.0	5.5	8.2	1.1	5.5	20.5	41.5	5
Melampus .	slight to high tide cond.[2]		6	? high tide		4.5	high tide ?		5.5	7.2 high tide		5.5	21.5	44.5	6

b. The Depositing Shore Series.—The flats series intergrades more closely than the different associations of the rocks. The conditions characteristic of each association are most marked at low tide and these are summarized as averaged data in Table XVI. As might be expected the average salinity at low tide decreases regularly as one goes back on the flats. But this is the only factor considered that shows such a regular relationship. With the others the conditions over the sand bar approach those

[1] Estimated between tides.

[2] Estimated for purposes of comparison.

"Combined ranking" refers to the rankings given in Tables XIV. and XV. The final ranking is based on the preceding column.

of the open water most closely and the conditions in the intertidal associations at the back of the flats are normally most extreme, but in the middle regions the plant growth, mainly

TABLE XVI.

FLAT SERIES.

Showing the average salinity, oxygen content, temperature and pH of different animal associations of the flats as found in collections from the bottom, open water excepted, at low tide, except for salinity where both low and mid tides are averaged. Ordinal ranking is based upon variation from conditions prevailing in open water.

Associations.	Salinity.			Oxygen in c.c. per L.			Temperature.			pH.			Ranking.
	No. Collections.	Average.	Rank.	No. Coll.	Average.	Rank.	No. Coll.	Average.	Rank.	No. Coll.	Average.	Rank.	Sum of Ranks.
Open	13	3.12	1	12	5.17	1	10	21.1	1	15	8.0	1	4
Scoloplos fragilis	3	3.04	2	3	4.23	3	6	21.3	2	6	8.04	2	9
Phascolosoma	6	3.00	3	4	6.15	4	12	23.3	6	13	8.15	5	18
Scoloplos acutus	6	2.97	4	9	3.88	5	15	23.1	5	17	7.95	3	17
Thyone	6	2.91	5	6	4.85	2	9	22	3	8	7.9	4	14
Mya	5	2.88	6	1	3.72	6	7	24	7	7	7.7	6	25
Melampus	0	—	7[1]	2	1.88	7	2	22.5	4	2	7.3	7	25

eel grass, affects conditions so that the relationship is irregular. In the summation of ordinal rankings the effect of this confusion is shown.

The amount of range, Table XVII., also increases steadily as one passes back on the flats only in the case of the salinity measurements. The oxygen content and pH begin to increase in observed range as soon as the eel grass is encountered in the muddy sand association and reach their maximum range in the tall eel grass of the *Scoloplos acutus* grounds. The water temperatures also increase in range but become greatest in the low water of the marginal muck association. The surface in the older associations undoubtedly becomes much warmer when exposed to air and this must be particularly marked in the *Melampus* association where the surface of the ground may be exposed to the full glare of the afternoon sun with almost no protection from the scant growth of marsh grasses.

[1] See note at bottom of Table XV.

TABLE XVII.

FLAT SERIES.

Showing range of variation of temperature, oxygen content, salinity and pH near the surface in the open water and at or near the bottom in other associations. All tide stages considered. Ordinal ranking is based upon amount of variation and relative location of extremes.

Association.	Salinity in %.			Oxygen in c.c. per L.			Temperature.			pH.		Ranking.			
	Limits.	Range.	Rank.	Limits.	Range.	Rank.	Limits.	Range.	Rank.	Limits.	Range.	Rank.	Sum of Ranks.	Combined Ranking.	Final Ranking.
Open.....	3.02			3.93			20			8.0 −					
	3.14	0.12	1	5.43	1.50	1	22	2.0	1	8.0 +	0.1	1	4	8	1
Scoloplos fragilis....	2.99			3.91			20			7.6					
	3.10	0.11	2	4.63	0.72	2	24.5	4.5	2	8.25	0.65	2	8	17	2
Phascolosoma.....	2.97			4.21			21			7.7					
	3.10	0.13	3	10.39	6.18	4	27	6.0	3	8.5	0.81	3	13	31	3
Scoloplos acutus.....	2.88			trace			18			7.3					
	3.02	0.14	4	9.31	9.50	5	26.5	8.5	4	8.45	1.15	4	17	34	5
Thyone....	2.22			3.23			17			7.4					
	3.10	0.88	5.5	5.31	2.08	3	28	11.0	5	8.2	0.8	5	18.5	32.5	4
Mya.....	2.22			0.0[1]			19			7.1					
	3.10	0.88	5.5	4.86	4.86	6.5	28	9.0[2]	6	8.2	1.1	6	24	49	6
Melampus.	slight to high tide cond.		7	? high tide		6.5	? high tide		7	7.2 high tide		7	27.5	52.5	7

The relative position of the extremes in salinity is much the same as in the eroding shore series. At high tide the salinity is practically constant throughout, but at low tide the lower limit decreases regularly with distance from the open water. The relations of oxygen content, pH, and temperature at the bottom are exactly similar to those of the preceding series except that they are more striking.

The ranking in this series, as in Table XV, is based upon the amount of range combined with the relative location of the extremes. On this basis salinity, temperature, and pH arrange the series in order of the ecological age of the different associations. On the basis of oxygen content, the marginal muck association is much younger than is expected. The combination

[1] See note at bottom of Table XV.

[2] Water temperatures only considered.

of these rankings arranges these associations in order of their age but when combined with the rankings from average conditions shown in the preceding table, the marginal muck (*Thyone*) association is placed slightly earlier in the series than it belongs. Further data would probably adjust this arrangement.

At the surface of this series, the range of oxygen, pH and temperature is greatest in the *Scoloplos acutus* region. The mat of eel grass just at the surface at low tide allows a surface layer of very warm water to be found in the bright sunlight where it is supersaturated with oxygen and has a correspondingly high pH. The *L. litorea*, *S. luciæ*, *Bugula*, *C. convexa*, *B. alternatum*, *Molgula*, and *Botryllus*, which occupy this region must be very resistant to these extreme conditions. Under the most pronounced conditions few animals capable of moving are found at the surface.

The differences on the flats level off at high tide. The tide appears to come to the back of the flats over the surface of the more stagnant water which has remained behind during low tide, bringing lower temperature, higher salinity, lower oxygen content and lower pH. Thus two collections from the back of the flats in 4.5 feet of water on a flowing tide showed a specific gravity of 1.018 at the bottom and 1.022 at the surface. Obviously such conditions do not prevail long and by diffusion the gradients disappear. In the long eel grass (*S. acutus* association), the vertical gradient at low tide in one foot of water was found to be from 3.37 c.c. oxygen per liter to 10.39 at the surface. Three hours later in the same place in three feet of water of the new tide the gradient was from 7.03 at the bottom to 8.3 at the surface. Similarly a pH gradient of from 7.7 at the bottom and 8.7 at the surface became one of 8.0 to 8.1.

The condition of the water over the bottom of the flats at high tide tends to become uniform throughout all the associations. Thus at NW. Gutter Flats, collections made under typical high tide conditions showed a range of 0.1 in pH over the flats while at low tide the range at similar stations was over 1.2.

V. Discussion.

Sumner (1908) in discussing the study of the distribution of bottom living animals in the Woods Hole region considered

character of bottom, depth, temperature, salinity, purity of water and currents as the important factors in determining distribution. The first of these factors, character of bottom, is characteristically different in the associations of eroding and depositing shores. The former is characterized by the presence of firm places for attachment and difficult burrowing conditions; the latter, by the converse of these conditions. The substratum also serves largely in distinguishing between the different associations of each series.

The influence of depth as a factor in animal distribution in the region covered by these studies is not due to depth as such but to depth as assuring a constant supply of water. This is shown in the rockweed association where animals normally found below low tide level on the wharf pilings may live well above it when protected from drying and from high temperatures by the mat of rockweeds.

Temperature serves as a limiting factor for these associations, during the season of the year studied, in the tide pools and more particularly on the flats. There in the *Scoloplos acutus* association above the dense eel grass mats at low tide the high temperature (32° C.) that may be reached must serve to kill off the more sensitive sessile animals as it drives the motile ones below the surface layer to the cooler water in the shade of the eel grass. The temperature to which animals may be exposed at low tide increases as one leaves open water conditions in both series. The effect of this high summer temperature of the flats as a factor limiting the geographic distribution in this region will be discussed in Study IV.[1] of this series.

In the associations studied, the salinity regularly increased as one approached open water conditions. The low salinity on the back part of the flats particularly in the *Melampus*, *Mya* and *Thyone* associations must serve as a limiting factor. These are subjected to such extreme ranges of salinity following heavy rains, particularly if these rains come at low tide and where there is some considerable surface drainage, that sensitive animals or animals in a sensitive stage in their life history must needs be killed or driven off.

In the locations studied, there was no contamination from

[1] In press in *Ecology*.

sewage wastes, so this possible factor in distribution may be dismissed.

The effects of tidal currents are well illustrated in the gutters and creeks of Hadley Harbor. These protected channels, supplied with constantly changing water which differs from open water only by the effect of coming over large tracts of submerged vegetation, support a wholly different animal life from that present where such currents do not enter. These locations are in the exposed rock or the rock-rockweed stage of development, in place of the *Mya* or *Melampus* stage which they would occupy if the currents were absent. In addition to these scouring effects of tidal currents, they have the well known function of oxygen and food carriers. They also eliminate the depth gradients in oxygen and pH found commonly in the stagnant water of the older associations.

The relation of oxygen and pH of the sea water to animal distribution has received no attention in the Woods Hole region. Both depend (1) on the supply of offshore water, (2) the amount of photosynthesis being carried on nearby, and (3) the character of the bottom. In the open water these factors depend upon currents and the proximity to vegetation. In the presence of vegetation oxygen is given off and the pH is increased. Muck absorbs oxygen and lowers the pH while sand has no effect on either unless it has been laid bare, when it, as well as rocks under similar conditions, decreases the pH without affecting the oxygen supply. Wave action has the converse effect.

From examining data from such regions as the rockweed or eel grass one might be tempted to generalize and say that as the oxygen increases the pH likewise increases and *vice versa*. Such a conclusion at best holds only in regions of abundant vegetation or of muck, and there the pH changes lag behind changes in oxygen concentration.

If the invertebrates are as sensitive to pH variations as Powers found herring to be, this correlation of high hydrogen ion concentration with the low oxygen regions of the muck must serve to keep free moving animals out of such conditions. Such action, combined with its greater regularity of distribution and slower fluctuations, makes the pH of the water more important

in such studies as the present than is the distribution of oxygen.

Both factors, however, may range widely within a given association. Take for example the sensitive *Amaræcium* association which flourishes on wharf pilings or on exposed rocks. At the mouth of Northwest Gutter, where the pH stays about 8.0 and the oxygen ranges from 3.72 to 4.95 c.c. per L., the rocks support a typical rock-*Amaræcium* association. Yet the same association, fully as rich in species, occurs at Gansett on similar rocks, but with much plant life all about and with the pH varying from 8.0 to 8.3 and the oxygen from 5.15 (and probably lower) to 8.56 c.c. per L. It will be noted that the range of conditions either at Northwest Gutter or at Gansett is lower than when the two are combined, so that, while the association can exist in these limits, it is not subjected to these extremes in one locality. The total range in both temperature and salinity is likewise greater when the two locations are considered together than when either is taken singly.

It is probable that a collection of data concerning the conditions under which the different sensitive animals live in all their different localities would, when thrown together, indicate that they could stand widely differing concentrations of all the water factors considered; when, as a matter of fact, they are exposed to relatively slight changes in the location in which they do live.

With less sensitive animals the association limits as set out in this paper mean nothing. *Pagurus longicarpus* apparently roams at will in all of those of the flats and occurs among those of the rocks, carrying with him, willy-nilly, his commensals. The mud snail, *Nassa obsoleta*, is at present found among all the associations, from the clean sand to the inter-tidal associations, and, according to Dimon, originally dominated the sand also before being driven off by *Littorina litorea*. In part it is able to do this because it is a resistant animal and in part on account of the fact that it probably becomes accustomed to conditions in a given locality and tends to keep within them. In this regard, one can but express the wish for more studies like that of Dimon. With a series of such studies at hand one could draw definite conclusions where now, so far as individuals are concerned, he is limited in large part to theorizing.

There is so much work necessary in making an ecological

survey that there is always a lively interest in single factor indices of associations, and at the beginning of the present studies I rather expected to find such an index in the pH relations. While a combination of the average pH, the extent of range and the relative position of the extremes does allow one to place these associations in their natural order with considerable exactness, and while such data is very suggestive it does not classify these associations with the precision necessary for a successful single factor index. This is emphasized in the rock series of associations, Tables XIV. and XV.

The use of the oxygen content of the water is out of the question as such an index of an association. Temperature is an aid but needs confirmation. Salinity, whether average or range, considered with position of extremes, does arrange the different associations in their logical order, and so qualifies for the recommendation that was predicted for pH, as the best single index when water conditions alone are considered. The readily determined factors of salinity, temperature and pH taken together give a much stronger index than any one of them alone.

If, however, on account of urgent haste, I should be forced to make use of a single criterion to divide the communities of the Woods Hole littoral, I should depend more on observation of the character of the sea bottom than on any other one factor.[1] This, the most obvious, the longest used, is still the least treacherous single factor index of littoral distribution in this region. It should be used with discretion since a rock well back on the flats supports a different set of animals from one on an exposed point, but the corrections are more obvious and more easily applied.

All the data collected in the present investigation agree in supporting the common sense conclusion that animal associations in a region such as this under consideration are not normally limited by any one factor, but by the interaction of several, and when feasible all these should be analyzed and recorded.

[1] Shelford ('14) in writing of the suitability of water for fishes concluded that the amount of clean bottom, the amount of carbon dioxide and the amount of hydrogen sulfide, taken together serve as an index of availability of bays and enclosures of the seas for fish life. Longley ('22) in studying the local distribution of Tortugas fishes concludes that the local distribution of many species is determined by the character of the bottom. This holds particularly for what he calls the "sand-patch" association.

The ecological age of the different associations has been repeatedly mentioned. This idea clearly and repeatedly stated by such workers as Cowles, Shelford and Adams, is apparently not yet fully understood. Briefly, it means that the *Melampus* association as it exists at present is an old association which has passed successively through the other stages standing before it in the series. Thus at one time the spot on which a *Melampus* association is now located was bare sand, which, as it became finely ground and somewhat packed, began to support a *Scoloplos fragilis* colony much as is found on Blind Gutter Bar at the present time. With accumulation of the organic products of these animals in the absence of a scouring current, other animals came in until the *Scoloplos fragilis* association began to resemble a *Phascolosoma* association. As more muck was deposited the older associations were passed one by one until the present old *Melampus* association resulted. With further deposition the land will be raised above tidal level and the *Melampus* association will gradually give way to strictly land animals. In this region the muck that accumulates is almost entirely of organic origin (cf. Survey, p. 32) so that the animals themselves have played a considerable part in causing ecological succession to take place.

Transitional stages between the different associations are abundant. A particularly noticeable one was studied that belongs between the *Scoloplos acutus* and *Thyone* associations. This is located near the gravel spit at the Uncatena side of the Northwest Gutter passage. There the *Scoloplos acutus* occur in the muck, but *Thyone* are absent as yet, although they are found nearby in greater numbers each year. Of the eight comparisons that have been made in the summary tables, four would place this location with the *Thyone* association, three place it as younger than *Phascolosoma* association, and the other with *Scoloplos acutus* where it belongs according to its animal inhabitants, and according to the average of these physical factors.

The wharf pilings present a specialized *Amaræcium* type of association that is obviously younger than the rock-*Amaræcium* community, although closely related to it both in animals present and in physical conditions. It represents more nearly the type of habitat that might be found where large rocks extend up out

of deep inshore water. Being a man-made habitat it is not, strictly speaking, a part of the rock series and is included in that series because it does give approximately the same condition that would be found on the rocky pillars just mentioned.

The succession of forms in this association can readily be studied. Glass slides placed under wharfs furnish a convenient method of finding the first pioneers to be expected. Observation of the growth of communities on new non-creosoted pilings and comparison with those on middle aged and old pilings would give the whole story for the wharf pilings, since they will of course never become a *Mya* association, as a rock-*Amaræcium* association may, or in the same way that its rock pillar prototype might.

In addition to such a study as this and to the studies of the ecology of individual species, in order to describe completely the littoral ecology of this region, studies should be made in the late autumn, early spring and in late spring or early summer. This last is particularly needed to round out our knowledge of the physical and faunistic conditions in these associations during the spring reproductive period.

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